

A REVISION OF THE GENUS
DINOTOPTERUS BLGR. (PISCES, CLARIIDAE)
WITH NOTES ON THE COMPARATIVE
ANATOMY OF THE SUPRABRANCHIAL
ORGANS IN THE CLARIIDAE

• FEB 1961

PRESENTED

BY

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INTRODUCTION

THE genus *Bathyclarias* was created by Jackson (1959) to accommodate ten endemic species of predominantly deep-water Clariidae from Lake Nyasa. Anatomical work which I have carried out on Jackson's material, and on other specimens, leads me to conclude that *Bathyclarias* does not differ substantially from the genus *Dinotopterus* (Boulenger, 1906). At present, *Dinotopterus* is a monotypic genus confined

to Lake Tanganyika ; a second species, *D. jallae* G. & T., 1917 from Southern Rhodesia should be referred to the genus *Clarias* (R. A. Jubb, personal communication).

THE GENERA *DINOTOPTERUS* AND *BATHYCLARIAS*

No comprehensive definition of *Dinopterus* has been published. Combining published descriptions and observations on specimens of *D. cunningtoni*, the genus can be distinguished from other clariids by the following characters : sides of head incompletely enclosed by bone, there being an appreciable gap between the supraorbital, dermosphenotic and sphenotic bones ; eyes laterally placed, forming part of the head outline when the fish is viewed from above ; no arborescent organs present in the suprabranchial chamber (this character was first observed by Poll [1953] ; other accounts of the genus [David, 1935 ; Marlier 1938 ; Bertin & Arambourg, 1958] imply that the arborescent organs are well developed) ; a small adipose dorsal fin present.

The last character calls for some comment. In all but the smaller specimens of *D. cunningtoni*, the fin is poorly developed ; it is little more than a slightly thickened and humped upper margin to the caudal peduncle. However, contrary to Boulenger's opinion, the fin is supported by the elongated neural spines of the posterior caudal vertebrae. These spines are c. 1·3–1·5 times longer than those of the preceding vertebrae. Thus, although superficially the adipose dorsal fin of adult *D. cunningtoni* is not a striking character, its presence is clearly manifest in the underlying bony structure.

The most outstanding morphological characters of *Bathyclarias* are the laterally placed eyes and the greatly reduced or even non-existent arborescent organs ; that is to say, characters which distinguish *Bathyclarias* from *Clarias* but not from *Dinopterus*. Only two characters given by Jackson (op. cit.) seem to separate *Bathyclarias* and *Dinopterus*, namely "sides of head enclosed in bony shields" and "... no adipose fin present." The former is not correct ; the arrangement of the lateral roofing bones in all species of *Bathyclarias* conforms to the *Dinopterus* pattern, with a large space separating the supraorbital, dermosphenotic and sphenotic bones. The thickened cephalic skin gives a superficial appearance of continuity but when the skin is removed, the true relationship of the bones is revealed.

The question of presence or absence of an adipose dorsal fin is more equivocal. Species referred to *Bathyclarias* show considerable variation in the posterior extension of the dorsal fin ; in some, it is narrowly separated from the caudal whilst in others there is a longer gap. In none is the distance separating the two fins as great as it is in *Dinopterus cunningtoni*. I have examined all the available material of *Bathyclarias* and conclude that in some (those with the greatest dorsal-caudal interspace) a weakly developed adipose fin is visible externally. In these fishes the upper caudal peduncle margin is thickened and, in a few, its outline is slightly humped. In none is the adipose fin as obvious as in *Dinopterus cunningtoni* of the same size. However, the osteological picture is more convincing. I have examined radiographs of two *Bathyclarias* representing species with long and short dorsal-caudal interspaces. In both species the most posterior caudal vertebrae have elongate neural spines

which are clearly longer than those of the preceding vertebrae underlying the rayed dorsal. Comparison between the more posterior caudal vertebrae of *Dinotopterus cunningtoni* and the two *Bathyclarias* species shows that the latter have relatively shorter neural spines ($c. 1.3 \times$ longer than the preceding spines; cf. $1.3-1.5 \times$ in *D. cunningtoni*). Despite these differences, I consider that the state of caudal peduncle development represented in the two *Bathyclarias* species serves to bridge the gap between the presence and absence of an adipose fin.

An identical situation exists within the genus *Clarias* (see David op. cit.). Here, three species of the subgenus *Heterobranchoides*, *Clarias mellandi* Blgr., *C. ngamensis* Casteln., and *C. pentissgrayi* (Fowler), all exhibit traces of an adipose fin. Again, the fin is poorly differentiated externally but is supported by elongate neural spines. The osteology of the skull in these fishes is typically that of a heterobranchoid *Clarias*, as is the condition of the hypertrophied suprabranchial arborescent organ (*C. ngamensis* and *C. mellandi* from personal observations, *C. pentissgrayi* from Fowler's [1931] description which does not include the suprabranchial organs). Certainly the "adipose" fin in *C. mellandi* and *C. ngamensis* is comparable, externally, with the dorsal thickening of the peduncle found in many *Bathyclarias* species. Furthermore, the condition of the supporting neural spines in *C. mellandi* (the only species examined for this character) is comparable with that found in the *Bathyclarias* species mentioned above.

Thus it seems that the presence or absence of a small adipose dorsal fin can no longer be considered sufficiently trenchant to warrant its use as the sole criterion for separating *Dinotopterus* and *Bathyclarias*.

One other point may be touched upon here. That is, the condition of the suprabranchial organ in the two "genera". In *Dinotopterus cunningtoni* the arborescent organs, so characteristic of the genus *Clarias*, are not developed, even in the largest specimens. In *Bathyclarias* the various species provide examples of development covering the entire range, from complete absence through simple stumps and sparsely branched "trees" to arborescent organs closely approaching the *Clarias* type in size and complexity. This wide range of variation in suprabranchial structure is described and discussed on p. 231-240.

If all these characters are considered, there seem to be no anatomical grounds for recognizing two genera and I propose to treat *Bathyclarias* Jackson, 1959 as a synonym of *Dinotopterus* Blgr., 1906, a redescription of which is given below.

THE GENUS DINOTOPTERUS BOULENGER, 1906

Dinotopterus Blgr. 1906, *Trans. zool. Soc. Lond.* 17 : 550; *Idem. Cat. Afr. Fish.*, 1911, 2 : 276; David, 1935, *Rev. Zool. Bot. Afr.* 28, 95 (misspelt *Dinopierus*). *Clarias*, part (*C. nyasensis* and *C. longibarbis*) Worthington, 1933, *Proc. zool. Soc. Lond.*, 285. *Bathyclarias* Jackson, 1959, *Proc. zool. Soc. Lond.* 132 : 109-138.

TYPE SPECIES. *Dinotopterus cunningtoni* Blgr., 1906.

Clariid fishes with the lateral roofing bones of the skull not forming a continuous casque because the supraorbital, sphenotic and dermosphenotic are separated by a

distinct space. Eyes lateral, forming part of the head outline when viewed from above. Dorsal and caudal fins separated by a distinct space which, at least superficially, shows all stages of intergradation between a weakly-developed adipose fin and the complete absence of such a fin; whether the fin is clearly developed or not, the more posterior caudal vertebrae have relatively elongated neural spines.

Suprabranchial chamber always present, as are the "gill-fans" forming its lateral and ventral walls; suprabranchial arborescent organs variously developed, from completely absent to moderately large and much branched.

DISTRIBUTION. Lakes Tanganyika and Nyasa: essentially a lacustrine genus, rarely occurring in streams and rivers.

THE LAKE TANGANYIKA SPECIES,
DINOTOPTERUS CUNNINGTONI BLGR., 1906

This species was recently redescribed by Poll (1953); in this description he remarks that the suprabranchial cavity is without arborescent organs. In general, this statement is correct but requires some amplification. None of the specimens I have examined possesses large or many-branched trees of the *Clarias* type, but a small stump or knob may be present on the fourth gill-arch of both large and small fishes. In some small specimens this structure is relatively large and bifid, occupying a fair volume of the cavity; in others, it is reduced to a slight swelling. No external indication of a knob is apparent in fishes with a head length of less than 0·7 cm. (at which size the "gill-fans" are still incompletely developed). In four specimens with head lengths of 1·4–3·5 cm. a well-developed knob is present on the epibranchial of the fourth arch. The next largest specimen available (standard length 17·5 cm.; head 4·7 cm.) has completely developed "gill-fans" but no trace of an arborescent organ.

Of particular interest is an apparently ontogenetic change in the histology of the suprabranchial epithelium (see p. 235 for a full explanation of the terms used). In young *D. cunningtoni* (smallest fish examined, 11·8 cm. S.L.) the gill tissue in this epithelium is arranged in the "Clarias" pattern of regular but sinuous lines or lamellae. Such is also the condition in fishes up to 17·5 cm. S.L. But, in the next larger specimen (46·5 cm. S.L.) and in all larger fishes, the lamellae are arranged in the "coralline" pattern of small circular patches of gill-cells. Unfortunately, I have not found any specimen in an intermediate condition, although in two of the smaller fishes (12·5 and 17·5 cm. S.L.), a few lamellae are in the form of elongate ovals. These could be interpreted as having arisen from the union of two neighbouring lamellae in a "Clarias"-type pattern. Subsequent development may involve the fractioning, by union at several points, of these ovals.

The only other *Dinopterus* species (*D. worthingtoni*) for which a wide size range is available, does not show any difference in lamellar pattern between large and small fishes. Because the adult size of *D. worthingtoni* is considerably less than that attained by *D. cunningtoni*, ontogenetic changes might take place at a size smaller than any represented in the collection.

THE SPECIES OF *DINOTOPTERUS* OCCURRING IN LAKE NYASA

Jackson (1955 and 1959) gave the first detailed account of the remarkable species-flock of Clariidae in Lake Nyasa. In his later paper, he drew attention to several taxonomic points which still required further study. On the basis of Jackson's original material, supplemented by other specimens collected by J. F. R. O., the Survey party of 1939 and Dr. Rosemary Lowe-McConnell, I have been able to investigate these points and also expand the descriptions of certain species.

My primary interest in the Nyasa *Dinotopterus* lay in their peculiar suprabranchial organs (see p. 232); when more material became available it was clear that the condition of these structures was more variable, both inter- and intraspecifically, than I had led Mr. Jackson to believe (see Jackson, 1959, p. 112). Furthermore, the suprabranchial organ showed itself to be a character of some taxonomic importance. A brief description of the suprabranchial region is now given for each species and should be read in conjunction with Tables I and II, and with the detailed account on pp. 231-240. Certain new descriptive terms are defined in that section.

Dinotopterus nyasensis (Worthington), 1933

Clarias nyasensis Worthington, 1933, Proc. zool. Soc. Lond., 308, fig. 9.
Bathyclarrias nyasensis (part), Jackson, 1959, Proc. zool. Soc. Lond. 132: 113.

Lectotype. B.M. (N.H.) Reg. No. 1932.11.15. 584.

The so-called "smooth-headed" form of this species (Jackson, 1959) is now recognized as a distinct species (see p. 222). Within *D. nyasensis* as defined here there is considerable variation in the roughness of the skull. Three small specimens, (27, 33 and 39 cm. S.L.) have the roofing bones almost completely smooth except for a few scattered tubercles on the occipital and frontal regions of the skull. In larger fishes the skull is entirely rugose, but in the largest specimen examined the rugosity is like that of the three smallest fishes. Such cyclical ontogenetic changes in skull ornamentation seem common amongst the larger Clariidae (personal observations).

As the additional material does not otherwise differ from the descriptions given by Worthington (1933) and Jackson (1953) a full redescription of the species is not warranted.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large; its length is about 33% of the head in fishes 49-62 cm. standard length (see also Table II). The arborescent organs, on the other hand, are poorly developed. In a fish of head length 20 cm. the tree on gill-arch II is polyfid and about 12 mm. high, that on arch IV about 16 mm. high and more extensively branched. In a smaller individual (H.L. 8.3 cm.) no tree is developed on the second arch and that of the fourth arch is a low, bifid stump. Such variability is not entirely size-correlated; for example, a specimen of 21 cm. head length has trees substantially less developed than another individual of 18 cm. H.L. In this fish, the trees are almost as well developed as in a specimen of 23 cm. head length.

The epithelium lining the suprabranchial cavity is highly vascular and the gill-like tissue is distributed in the "Saccobranchus" pattern (see p. 235).

Dinotopterus jacksoni sp. nov.

Bathyclarias nyasensis (part), Jackson, 1959, *Proc. Zool. Soc. Lond.* **132** : 113 (the smooth-headed forms only).

Bathyclarias loweae (part). *Idem, ibid.*, 114, fig. 1B.

HOLOTYPE. A fish 61 cm. standard length, from Nkata Bay; B.M. (N.H.) Reg No. 1960.2.29.26.

DESCRIPTION. Based on the holotype, two entire specimens 46 and 68 cm. S.L., and one head 23·3 cm. long.

Length of head contained 3·1–3·8 times in standard length, the dorsal surface smooth or relatively smooth; when present, the rugose areas are most apparent on the posterior and antero-lateral regions of the skull. In large specimens the squamosal region (i.e. the sphenotic and pterotic bones) is slightly domed; the intervening occipital region is flat. Frontal and occipital fontanelles barely visible beneath the thick cephalic skin; the frontal fontanelle very narrow, the occipital fontanelle almost circular. Head broad, its width contained 4·4–4·9 times in standard length and 1·4–1·6 times in head length. Eye lateral, its diameter 15·8–18·8 in head length and 9·8–10·5 in the interorbital width, which is contained 1·6–1·9 times in head length and is about equal to the width of the mouth. Dorsal outline of the snout rounded; snout length contained 3·7–4·4 in the head.

Barbels smooth, the base of the maxillary pair somewhat fleshy. Length of nasal barbel 1·9–4·5 in head; maxillary barbel 1·3–1·7, outer mandibular 1·3–2·8, inner mandibular 2·2–5·3 in head. Barbel length shows negative allometry with head length.

Premaxillary and vomerine teeth fine and pointed; length of half the premaxillary band 4·7–5·2 in head length, that of half the vomerine band 5·0–5·9; vomerine band interrupted in the mid-line, its width equal to or slightly less than that of the premaxillary band.

Gill rakers long (almost equal to the longest gill filaments) and numerous, 172–230 on the first gill-arch, the number showing positive correlation with standard length. In preserved material the gill filaments are colourless.

Dorsal fin with 64 rays, the distance between its origin and the supraoccipital contained 3·8–4·6 times in head length. Anal with 44 rays. Both fins are clearly distinct from the caudal. Pectoral fins short and covered with thick skin, the anterior face of the spine weakly denticulate or smooth; greatest length of the pectoral contained 2·2–2·8 in head length. Caudal peduncle as long as deep to 1·4 times deeper than long. Adipose dorsal weakly developed.

Vertebral (excluding the fused anterior mass) in the single specimen radiographed (the Type), 54.

I have great pleasure in naming this species after Mr. P. B. N. Jackson, who first recognized that certain specimens he referred to *Bathyclarias nyasensis* might represent a new species.

SUPRABRANCHIAL ORGANS. The suprabranchial chamber is moderately large (its length c. 32% of head; see Table II for volumes) and the gill-fans are well-developed. The arborescent organs are greatly reduced. In the three largest speci-

mens there is no macroscopic indication of an anterior tree and the posterior one is represented by a simple, short phallic outgrowth. There is no posterior tree in the smallest specimen (S.L. 46 cm.) but there is a small stump occupying the usual site of the anterior tree.

Gill tissue in the suprabranchial epithelium is arranged in the "Saccobranchus" pattern. A striking feature in the histology of this epithelium is an abundance of large mucous cells widely distributed amongst the gill tissue and the undifferentiated epithelial cells.

DISCUSSION. From Jackson's arrangement of the Nyasa species now referred to *Dinotopterus*, *D. jacksoni* is closely related to *D. nyasensis* and *D. loweae*. Indeed, specimens of *D. jacksoni* were previously included in both these species, although Jackson did stress the possibility that smooth-headed specimens of *Bathyclarias nyasensis* might represent a distinct species. At first sight the virtually smooth head of *D. jacksoni* seems a distinctive character, but as Jackson noted, this condition intergrades with that occurring in large *D. nyasensis*. Also, the skull of the smallest *D. jacksoni* specimen is as rough as that of a comparably sized *D. nyasensis*. From the examination of numerous *Clarias mossambicus* skulls and the skulls of most *Dinotopterus* species, it seems that the degree of rugosity is chiefly dependent on the size of the individual. The smooth-headed *D. gigas* may prove exceptional to this generalization (see also p. 221).

The principal difference between *D. nyasensis* and *D. jacksoni* lies in the greatly reduced suprabranchial structure of the latter. Although the arborescent organs of *D. nyasensis* are reduced, in no adult specimen is the reduction so marked as in *D. jacksoni*.

Two other, less pronounced, differences are the shorter pectoral fins of *D. jacksoni* and the tendency in this species for the squamosal region of the skull to become domed.

Even though *D. jacksoni*, *D. loweae* and *D. nyasensis* are closely related on "key" characters, I do not think that this reflects the phyletic relationship of the species; more material is required, however, before this problem can be investigated.

Dinotopterus loweae (Jackson), 1959

Bathyclarias loweae (part) Jackson, 1959, Proc. zool. Soc. Lond. 132 : 114, fig. 1A.

One of the two specimens from which the original description was made is now referred to *D. jacksoni*. The redescription is based on the holotype (82 cm. S.L.), two other fishes 71 and 72 cm. S.L. and two heads 17·0 and 17·6 cm. long. A juvenile specimen 19·5 cm. S.L. is tentatively determined as *D. loweae*, but is not included in the description.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.3 from Nkata Bay.

DESCRIPTION. Length of head contained 3·1-3·7 times in standard length, its dorsal surface moderately rugose on the posterior half, smooth anteriorly. Head width contained 4·9-5·3 times in standard length and 1·4-1·7 times in head length. Eye diameter 14·2-18·0 in head length and 6·9-10·3 in interorbital width (showing

negative allometry with head length). Interorbital width 1·8–2·1 in head length, snout length 3·5–4·4; distance between anterior nostrils 3·5–4·2 times. Barbels smooth; length of nasal barbel 3·0–4·3 in head, maxillary barbel 1·3–1·7, outer mandibulars 1·9–2·2, inner mandibulars 2·7–3·7 in head.

Premaxillary and vomerine teeth fine and pointed, length of half premaxillary band contained 4·5–5·7 times in head length, that of half vomerine band 4·5–6·5 times; vomerine band interrupted in the mid-line, its width equal to or slightly greater than that of the premaxillary band.

Gill rakers numerous and fine, from 180 (in fishes of 15·6 cm. H.L.) to 260 (H.L. 23·2 cm.); length 0·7–1·0 of the length of the longest gill filament (see also Jackson, 1959, p. 113).

Dorsal fin with c. 63–65 rays, the distance from its origin to the occiput contained 3·7–4·9 times in head length. Anal fin with 49–54 rays. Caudal peduncle 1·1–1·5 times as deep as long.

The strongly humped body of the holotype is less marked in other specimens and may thus be correlated with size or may be due to *post-mortem* muscular contraction.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large (see Table II) and the arborescent organs well developed and much branched in all the specimens examined. In the smallest fish (a specimen 19·5 cm. S.L. and only tentatively placed in this species) the future anterior tree appears as a low swelling on the second gill-arch whilst the posterior tree is four-branched and is 3 mm. high.

Gill tissue in the suprabranchial epithelium is arranged in the "Clarias" pattern (see p. 235).

Dinotopterus illesi (Jackson), 1959

Bathyclarrias illesi Jackson, 1959, Proc. zool. Soc. Lond. 132 : 116, fig. 2.

HOLOTYPE. A male 66 cm. S.L. from Nkata Bay, B.M. (N.H.) Reg. No. 1960. 2.29.8.

This description is based on the holo- and paratypes (66 and 59 cm. S.L. respectively) and one other specimen, 69 cm. S.L.

Length of head 3·2–3·3 in standard length, the dorsal surface rugose in the smaller specimens, smoother in the largest fish. Head width 4·7–5·1 in standard length and 1·4–1·6 in head length. Eye diameter 16·0–19·6 in head length and 10·0–10·5 in interorbital width, which is contained 1·7–1·9 times in the head. Snout length 3·9–4·1; distance between anterior nostrils 3·7–3·9 in head.

Barbels smooth, base of the maxillary barbel somewhat swollen. Length of nasal barbel 4·1–5·7, maxillary barbel 1·8–2·1, outer mandibular 3·7–4·8, inner mandibular 2·4–3·1 in head length.

Premaxillary and vomerine teeth fine and pointed, length of half premaxillary band about 5 in head. Vomerine band interrupted in the mid-line and slightly narrower than the premaxillary band, its half length contained 4·5–5·0 times in the head.

Gill rakers c. 0·8 length of longest gill filament; 170–184 on the first arch. Filaments dark, purplish-black (cf. *D. atribranchus*, *D. filicibarbis* and *D. worthingtoni*).

Dorsal fin with 65–67 rays, rather narrowly separated from the caudal; distance between its origin and the occipital process contained 3·8–4·5 times in the head length. Anal fin with 50–52 rays. Caudal peduncle 1·1–1·6 times as deep as long.

The "black removable mucus over the body" which Jackson notes, is not easily discernible in preserved material.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is large (see Table II), the arborescent organs present and much branched. There is considerable individual variation in the size of the trees; those of the type (66 cm. S.L.) are much smaller than the trees in the paratype (59 cm. S.L.).

Gill tissue in the lining epithelium is arranged in the "Saccobranchus" pattern (see p. 235).

Dinopterus longibarbis (Worthington), 1933

Clarias longibarbis Worthington, 1933, Proc. zool. Soc. Lond. 309; fig. 10.

Bathyclarias longibarbis, Jackson, 1959, Proc. zool. Soc. Lond. 132: 117.

HOLOTYPE. A male 75 cm. S.L. B.M. (N.H.) Reg. No. 1932.11.15. 592.

DESCRIPTION. Based on the holotype and two other specimens, 44·5 and 40·5 cm. S.L.

Length of head 3·4–3·7 in standard length, dorsal surface rugose, especially over the posterior two-thirds. Width of head contained 1·4–1·5 in head length. Eye diameter 14·0–14·7 in head length, 7·4–8·8 in interorbital width which is contained 1·6–1·9 in head. Snout 3·5–3·6 in head length; distance between anterior nostrils 3·6 times.

Barbels long and smooth, length of nasal barbel contained 1·1–1·6 times in head, maxillary and outer mandibular barbels respectively 1·2–1·3 and 1·1–1·2 times as long as the head; inner mandibular barbels 1·2–1·6 in head. It is interesting to note that the negative allometry of barbel length with standard length usual in other species is not at all marked, despite the size discrepancy between the type and the two smaller specimens.

Premaxillary and vomerine teeth fine and pointed, half length of either band contained about 5 times in head length. Vomerine band narrowed medially but continuous in two specimens, interrupted in the third, its width slightly less than that of the premaxillary band.

Gill rakers relatively short, about 0·5–0·6 of the length of the longest gill filaments; there are, on the first gill arch, 145 rakers in the type (75 cm. S.L.); 90 and 83 rakers in the two smaller fishes (S.L.'s 44·5 and 40·5 cm. respectively).

Dorsal fin with c. 65 rays, distance from its origin to the occiput contained 5 times in the head. Anal fin with c. 56 rays. Caudal peduncle 1·4 times as deep as long.

SUPRABRANCHIAL ORGAN (see also Table II). A good ontogenetic series is provided by this material. The type specimen has large, polyfid arborescent organs on both the second and fourth arches. In the fish 44·5 cm. S.L., the anterior tree is merely a stub, whilst the posterior tree is small, with seven branches. A similar developmental state is seen in the 40·5 cm. fish, except that the anterior tree is even less developed.

Gill tissue in the suprabranchial epithelium is distributed in the "Clarias" pattern.

Dinotopterus rotundifrons (Jackson), 1959

Bathyclarias rotundifrons Jackson, 1959, Proc. zool. Soc. Lond. 132 : 118, fig. 3.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.11, from Nkata Bay.

As there are no additional specimens, reference is made to the original description.

SUPRABRANCHIAL ORGAN. The cavity is relatively small (see Table II) and the arborescent organs are greatly reduced. There is no macroscopic indication of an anterior tree and the posterior tree is represented by a single, phallic projection about 5 mm. high (i.e. in a specimen of 14.5 cm. head length).

Gill tissue in the suprabranchial epithelium is arranged in a "coralline" pattern (see p. 236).

Dinotopterus foveolatus (Jackson), 1955

Clarias foveolatus Jackson, 1955, Proc. zool. Soc. Lond. 125 : 681, text-fig.

Bathyclarias foveolatus, *Idem*, 1959, Ibid. 132 : 118.

The only information additional to that given by Jackson (op. cit.) concerns the structure of the suprabranchial organs.

Jackson was misled by the well-developed "gill fans" into stating "Accessory breathing organs present, as is usual in this family . . .".

The suprabranchial chamber of *D. foveolatus* is considerably reduced, its length being only about 20% of the head. There is a corresponding decrease in depth so that the chamber is noticeably shallow (see Table II). No appreciable reduction is apparent in the "gill-fans". The tree associated with the fourth gill arch is reduced to a small "T"-shaped outgrowth and there is no macroscopic indication of an anterior tree.

In preserved material the suprabranchial epithelium is jet-black except for the small patches of white gill tissue, distributed in the "coralline" pattern (see p. 236).

Dinotopterus euryodon (Jackson), 1959

Bathyclarias euryodon Jackson, 1959, Proc. zool. Soc. Lond. 132 : 120, fig. 4.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.13.

No further specimens have been obtained for study purposes.

SUPRABRANCHIAL ORGAN. In the single specimen (S.L. c. 104 cm.) I have been able to dissect, the cavity is not appreciably reduced (length c. 28% of head; volume 107 cc.) but there are no indications of arborescent organs. The gill-fans, on the other hand, are fully developed.

Because the specimen is poorly preserved it was difficult to get a clear histological picture of the suprabranchial epithelium. However, the gill tissue is apparently distributed according to the "Saccobranchus" pattern (see p. 235).

Dinotopterus filicibarbis (Jackson), 1959

Bathyclarias filicibarbis Jackson, 1959, Proc. zool. Soc. Lond. 132 : 120, fig. 5.

HOLOTYPE. B.M. (N.H.) Reg. No. 1955.6.14.1 from Nkata Bay.

No further specimens have been collected, but the original description must

be emended. In the holotype, at least after preservation, the gill filaments are greyish-black (cf. *D. ilesi* and *D. foveolatus*).

SUPRABRANCHIAL ORGAN. The cavity is long (*c.* 34% of the head) but shallow so that its volume, in the holotype, is 32 c.c. No arborescent organs are visible.

Gill tissue in the suprabranchial epithelium is arranged in the "coralline" pattern (see p. 236); the undifferentiated tissue is jet-black. Identical tissue occurs in *D. foveolatus*.

Dinotopterus worthingtoni (Jackson), 1959

Bathyclarias worthingtoni Jackson, 1959, Proc. zool. Soc. Lond. 132 : 123, fig. 6.

HOLOTYPE. B.M. (N.H.) Reg. No. 1960.2.29.18 from Nkata Bay.

No additional study material of this species has been deposited in the Museum. When re-examining the original specimens I found that the gill filaments of the two paratypes (25·4 and 27·5 cm. total length) are greyish-black, except at their extreme distal tips. Neither the small individuals (7·5 and 8·0 cm. S.L.) nor the large holotype (68·2 cm. T.L.) have dark filaments. It seems unlikely that such pronounced darkening of the filaments can be attributed to preservation or to any *post mortem* changes, such as a branchial haemorrhage. If both these explanations are discounted, there remains the suggestion that darkening of the gills can occur as an individual variation. The character might therefore be of reduced taxonomic importance. The gills of *D. ilesi*, *D. foveolatus* and *D. atribranchus* are black in preserved specimens, but as these species are known from very few specimens it is impossible to determine the intraspecific constancy of the character.

SUPRABRANCHIAL ORGAN. The cavity is somewhat reduced (see Table II). Ontogenetic changes in the development of the arborescent organs are clearly seen in these specimens. The trees are greatly reduced at all sizes; no anterior tree is developed, even in the largest fish (the holotype, 68·2 cm. T.L.), and in this fish the posterior tree is represented by a small knob about 3·5 mm. length. In a smaller specimen (23 cm. S.L.) the posterior tree is a weakly trifid knob, proportionately larger than that of the holotype. The smallest fish examined (6·6 cm. S.L.) shows a very early stage in suprabranchial ontogeny, at which no trees are visible and even the "gill-fans" are incomplete.

Gill tissue within the suprabranchial epithelium is distributed in the "Saccobranchus" pattern; no ontogenetic changes in pattern were detected (cf. *D. cunningtoni*, where such changes are found).

Dinotopterus gigas (Jackson), 1959

Bathyclarias gigas Jackson, 1959, Proc. zool. Soc. Lond. 132 : 125, fig. 7.

HOLOTYPE. A head and skin B.M. (N.H.) Reg. No. 1960.2.29.35.

Originally based on a single giant specimen 135 cm. S.L., the description must now be modified to include four smaller specimens (one head 28 cm. long and three entire fishes 47·0, 61·0 and 64·5 cm. S.L.).

Length of head contained 2·6–3·6 times in standard length, the dorsal surface

smooth and covered with thick skin; head width 3·9–5·0 in standard length and 1·3–1·4 in head length. Eye diameter 13·7–19·3 in head (showing negative allometry with head length) and 7·2–14·0 in interorbital width (again, negatively allometric). Interorbital width 1·3–1·9 in head, length of snout 3·3–4·3.

Barbels smooth, their length negatively allometric with head length; nasal barbel 2·7–6·0 in head, maxillary 1·1–2·3, outer mandibular 1·9–3·1, inner mandibular 2·5–4·2.

Premaxillary and vomerine teeth slender and pointed, half length of either band contained about 5 times in head length. Vomerine band continuous or interrupted medially, its width equal to or slightly greater than that of the premaxillary band.

Gill rakers short, 0·5–0·65 of the length of the longest gill filaments; 100–149 on the first gill arch, the number positively correlated with standard length.

Dorsal fin with c. 69 rays, anal with c. 56. Caudal peduncle as long as deep or, deeper than long.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is relatively reduced, particularly in large fishes (see Table II).

In the holotype (S.L. 135 cm.) both arborescent organs are of approximately equal size (an unusual feature but one possibly correlated with the great size of this fish) relatively large and extensively branched. These organs are of disparate sizes (the posterior tree larger) in a head 28 cm. long—estimated to be from a fish c. 90 cm. S.L.—and although small in relation to the volume of the cavity are much branched. The same condition is found in a fish 61 cm. S.L. but in a larger specimen (64·5 cm. S.L.) the arborescent organs are reduced to a small, bifid outgrowth on the second arch and a slightly larger, trifid structure on the fourth arch. In the smallest specimen examined (47 cm. S.L.) the anterior tree is represented by a small knob and the posterior tree by a large, sparsely branched outgrowth.

The gill tissue in the suprabranchial epithelium is arranged in the "Clarias" pattern (see p. 235).

Dinopterus atribranchus sp. nov.

HOLOTYPE. A male, probably adult, 39 cm. S.L. B.M. (N.H.) Reg. No. 1960.2.29. 17.

DESCRIPTION. Based on the unique holotype. Length of head 3·5 in standard length, the dorsal surface relatively flattened; roofing bones rugose, the tubercles arranged in definite patterns. Frontal fontanelle long and narrow, its length 3·7 in head. Width of head 5·2 in standard length and 1·5 in head length. Eye diameter contained 11·2 in head length and 4·8 in interorbital width, which is contained 2·3 times in head length. Length of snout 4·9 in head, distance between anterior nostrils 5·6 times.

Barbels smooth; length of nasal barbel contained 2·7 times in head length, maxillary 1·4, outer mandibular 2·0 and inner mandibular 3·3 times.

Premaxillary and vomerine teeth fine and pointed, the width of the vomerine band about three-fifths that of the premaxillary.

Gill rakers very short, about 0·3 of the length of the longest gill filament; 85 on the first gill arch. Gill filaments dark greyish-black.

Dorsal fin with c. 60 rays, anal with c. 45. Caudal peduncle slightly deeper than long, adipose dorsal very weakly developed.

Vertebrae (excluding the anterior fused mass) 54.

SUPRABRANCHIAL ORGAN. The suprabranchial cavity is reduced, the anterior tree a small stump and the posterior tree a short, six-branched outgrowth. The "gill-fans" are well developed.

Gill tissue in the suprabranchial epithelium is arranged in the "Saccobranchus" pattern (see p. 235).

DISCUSSION. Because this specimen is relatively small it is most likely that the low number of gill rakers is not definitive. On the other hand, the very short rakers may be looked upon as a character unaffected by growth. From Jackson's (1959) analysis of gill raker proportions in *D. nyasensis* and *D. worthingtoni*, and mine of *D. cunningtoni* (below) it is clear that very little change occurs in the relative length of the rakers, even over a wide size range. The gill rakers in *D. atribranchus* are remarkably short even for a species within the group having reduced rakers.

If the possession of black gill filaments is a good specific character (but see p. 227) then *D. atribranchus* is readily distinguished from all other species in the short-rakered group.

The condition of the suprabranchial organs in *D. atribranchus*, even though these probably have not completed their development, distinguishes the species from *D. rotundifrons*, *D. worthingtoni* and *D. euryodon*.

From *D. gigas*, *Dinotopterus atribranchus* is readily distinguished by its rugose skull (at least in the size ranges represented), shorter and narrower snout, and its wider interorbital region.

KEY TO THE SPECIES OF *DINOTOPTERUS*

This key has been built around that produced by Jackson (1959). Like most keys it is unsatisfactory especially since the known range of variation for many of the characters used blurs several of the dichotomies. Two particular points should be noted with care. One is the second dichotomy, based on the number of gill rakers and their relative lengths. I have examined a wide size-range of *Dinotopterus cunningtoni* and find that although the proportional measurement is constant at all sizes, the number of rakers shows a fourteen-fold increase in large fishes (see below). Similar results were obtained by Jackson (op. cit.) for *D. nyasensis* and *D. worthingtoni*.

Gill raker counts and proportional measurements for *D. cunningtoni*:

Head length (cm.)	Length of longest raker Length of longest filament	Number of rakers
0·7	0·5	12
1·4	0·7	20
1·7	0·7	20
4·7	0·5	55
13·1	0·5	147
16·5	0·7	175
19·3	0·7	200
26·0	0·7	172

From these figures it is clear that the relative length of the rakers is the more reliable "key character"; in larger fishes it is reinforced by the number of rakers.

The second unsatisfactory major dichotomy is the seventh, which is based on the relative length of the maxillary barbels. This measurement is known to show negative allometry with head length, so that small specimens of the species-group alternative to *D. longibarbis* will tend to show the *D. longibarbis* character.

References to the suprabranchial organs and the nature of the suprabranchial epithelium ("Clarias"-like or "Saccobranchus"-like) are discussed fully on pp. 232-7.

I have not used Jackson's character of "black, tarry removable mucus on body" to separate *D. illesi* from *D. nyasensis* because with preserved material this character is difficult to apply and may be misleading.

1.	Adipose dorsal fin poorly developed or apparently absent	2
	Adipose fin clearly discernible	<i>D. cunningtoni</i>
2.	Gill rakers on first arch 0.3-0.6 length of filaments, rarely more than 145 (at least in fishes 7-75 cm. S.L.)	3
	Gill rakers 0.7-1.0 length of filaments, more than 150 (usually 170-260) in specimens > 46 cm. S.L., fewer in smaller fishes	10
3.	Barbels rounded, smooth and simple	4
	Barbels flattened and broad, the maxillary and outer mandibular pair with rounded lappets distally	<i>D. filicibrabis</i>
4.	Body smooth, not pitted	5
	Body rough and pitted	<i>D. foveolatus</i>
5.	Gills and suprabranchial cavity black	<i>D. atribranchus</i>
	Gills and suprabranchial cavity not black	6
6.	Vomerine tooth-band less than 1½ times as broad as the premaxillary band; teeth fine, discrete and pointed	7
	Vomerine tooth-band more than 1½ times broader than the premaxillary band, teeth coarse and blunt	<i>D. euryodon</i>
7.	Maxillary barbel not reaching beyond the tip of the pectoral fin	8
	Maxillary barbel reaching well beyond extremity of pectoral fin	<i>D. longibarbis</i>
8.	Snout length contained less than 4.6 times in head length; dorsal outline of snout slightly curved; head not noticeably chubby	9
	Snout at least 5 in head, rounded. Head chubby	<i>D. rotundifrons</i>
9.	Base of maxillary barbel markedly conical, swollen and fleshy. Suprabranchial trees greatly reduced; only a small stump with 4 or fewer branches on the fourth gill arch, at least in fishes > 20 cm. S.L., absent in fishes, < 7 cm. S.L.	<i>D. worthingtoni</i>
	Base of maxillary barbel not markedly enlarged. Arborescent suprabranchial organs on second and fourth gill arches, at least in fishes > 45 cm. S.L., much branched in large fishes, sparsely branched in specimens 45-60 cm. S.L.	<i>D. gigas</i>
10.	Body relatively slender; maxillary barbel (at least in fishes 27-69 cm. S.L.) contained 1.8-2.2 in head	11
	Body stout; maxillary barbel 1.2-1.7 in head	12
11.	Gill filaments and epithelium of suprabranchial cavity purplish-black	<i>D. illesi</i>
	Gill filaments and epithelium of suprabranchial cavity colourless in preserved specimens	<i>D. nyasensis</i>
12.	Suprabranchial arborescent organs merely a simple stub on the 4th gill arch; suprabranchial epithelium of the "Saccobranchus" type. Dorsal surface of head with few rugosities	<i>D. jacksoni</i>

Suprabranchial arborescent organs moderately well developed on 2nd and 4th arches, much branched in specimens 50–80 cm. S.L. (but reduced to a small four-branched tree on the fourth arch in a fish 20 cm. S.L.) ; suprabranchial epithelium of the "Clarias" type *D. loweae*

THE SUPRABRANCHIAL RESPIRATORY ORGANS IN THE CLARIIDAE

Several descriptions of the suprabranchial organs have been published since the original but remarkably complete account of their anatomy given by E. Geoffroy St. Hilaire in 1802. This author's preliminary notes (published by Lacepède, 1836) describing the appearance of the organs and their probable respiratory function, still provide one of the most succinct accounts available.

Of the more recent papers, that of Rauther (1910), giving a detailed histological account, and that of Marlier (1938), providing a more general description, are the most comprehensive.

Variation in the suprabranchial region of the Clariidae is considerable (see below and also David, op. cit.: Poll, 1942; Greenwood, 1956 and 1959) but in the majority of species the following brief description is applicable.

Above the gill chamber there is a spacious cavity, enlarged posteriorly where it extends ventrally to about the level of the pharyngeal floor. The lateral floor and walls of the cavity are formed by certain modified and membraneously united, fan-like gill filaments on the upper part of each gill arch (hereafter referred to as the "gill-fans"). The entire chamber, excluding the fans, is lined with highly vascularized epithelium irrigated by afferent and efferent blood vessels from each gill arch. As might be expected, the "gill-fans" have the histological structure of gill filaments. A similar histology is shown by the epithelium lining the cavity (Rauther, op. cit. and personal observations).

Thus, as Carter (1957) emphasized with regard to the arborescent organs in *Clarias* (see below), the respiratory epithelium is not merely a direct modification of an unmodified internal surface. It is, in fact, a modification and extension of the normal branchial tissues. What at first sight appears to be the differentiation of typical gill tissue within unmodified epithelium during the ontogeny of the suprabranchial cavity (see below, p. 235), can be interpreted in a different way. The spatial relationships of the tissue to the gills is extremely intimate as is clearly seen in the embryo. This tissue could, therefore be considered as primarily branchial; if this is so, the relatively late appearance of gill cells could be interpreted as the delayed manifestation of its competence to develop into branchial tissue.

Contained within the cavity and occupying up to four-fifths of its volume are two much-branched arborescent structures (the "trees") developed from the epibranchials of the second and fourth gill arches. The epithelium covering the cartilaginous skeleton of each tree has the histological structure of gill tissue. It is supplied with afferent and efferent blood vessels from the corresponding gill arch.

In every *Clarias* species investigated the size and complexity of the arborescent organs are positively correlated with the size of the individual and, of course, with its ontogenetic stage. I have studied the complete ontogeny of the suprabranchial

organs in *Clarias mossambicus* and the following notes summarize my observations. For comparative purposes it should be noted that the modal adult size-range of *C. mossambicus* in Lake Victoria is 50–90 cm.

The arborescent organs develop late in post-larval ontogeny (Greenwood, 1956); a single knob associated with the fourth arch appears in fishes of c. 3 cm. length. The anterior tree (second arch) develops somewhat later. When the fish is about 5 cm. long, the posterior tree is trifid; branching then continues until the much-branched definitive condition is attained when the fish is about 30 cm. long. Development of the anterior tree follows a similar pattern but always lags behind that of the posterior one; ultimately it is about two-thirds the size of the latter. When fully developed, the two trees occupy 70–80% of the suprabranchial cavity.

Differentiation of gill tissue within the suprabranchial epithelium occurs before the appearance of the trees; suprabranchial lamellae first appear when the fish is about 1 cm. long.

The "gill-fans" are the last suprabranchial structures to develop and usually complete their differentiation from the gill filaments only after the macroscopic appearance of the posterior tree. Obvious morphological changes are, however, apparent in those filaments destined to form the "fans" at about the time of the first appearance of lamellae in the lining epithelium. Until the "fans" are fully developed, the suprabranchial cavity has wide openings into the branchial and pharyngeal cavities. The cavity must, therefore, be filled with water and in early post-larval fishes probably acts as an aquatic gill. Hora (1935) has shown that the lung-like air-sacs of *Amphiphnous* can be utilized in this way.

Suprabranchial respiratory organs are not well developed in all Clariidae and in some genera may be entirely absent. With one exception (the genus *Dinotopterus*), clariids with greatly reduced organs are small. Various stages in suprabranchial reduction are manifest by these genera and also in some of the smaller *Clarias* species (those belonging to David's subgenera *Clarias* (*Clarias*) and *C.* (*Allabenchelys*)).

THE SUPRABRANCHIAL ORGAN IN *DINOPTERUS*

Perhaps the most outstanding anatomical feature of the Lake Nyasa *Dinotopterus* species is the wide interspecific variation in the suprabranchial organ. Differences are most evident in the morphology of the arborescent organs but also appear in the histology of the suprabranchial lining epithelium. No other clariid genus shows such variation; I have examined seventeen *Clarias* species and found that, within any one of the three subgeneric groups, the degree of suprabranchial organization and development is remarkably constant. *Dinotopterus* stands in sharp contrast. Here one finds within a single species-flock some species in which both trees are present and fully developed, others with small, sparsely branched trees and finally, a large group of species in which no anterior tree is developed and the posterior tree is greatly reduced or even absent (see Table I). When polyfid arborescent organs are present, as in large *D. ilesi* and *D. gigas*, the trees are relatively reduced and occupy a smaller volume of the cavity than do the trees of adult *Clarias mossambicus* and other members of the *C. (Heterobranchoides)* subgroup. Such trees in *Dinopt-*

TABLE I.—*Types of Arborescent Organs and Suprabranchial Epithelium in Dinotopterus Species*

(1)	Arborescent organs present, relatively large and much branched	Suprabranchial epithelium*	Arborescent organs present, small and sparsely branched	Suprabranchial epithelium*	Arborescent organs absent or represented by a stub on 4th arch	Suprabranchial epithelium*
<i>Dinotopterus illesi</i>	•	Sb.	<i>Dinotopterus nyasensis</i> •	Sb.	<i>Dinotopterus filibravis</i> •	cor.
<i>Dinotopterus loweae</i>	•	Clar.	<i>Dinotopterus atribranchus</i> •	Sb.	<i>Dinotopterus euryodon</i> •	cor.
<i>Dinotopterus longibarbis</i>	•	Clar.			<i>Dinotopterus cumingtoni</i> •	cor.
<i>Dinotopterus gigas</i>	•	Clar.			<i>Dinotopterus worthingtoni</i> •	Sh.
					<i>Dinotopterus rotundifrons</i> •	cor.
					<i>Dinotopterus jacksoni</i> •	Sh.
					<i>Dinotopterus foveolatus</i> •	cor.

* Clar. = "Clarias"-type. Sb. = "Saccobranchus"-type.
cor. = "coralline"

TABLE II.—*Data on the Gill Area, Volume of the Suprabranchial Cavity and the Number of Filaments on the First Gill Arch of Certain Clarias Species Compared with those of Dinotopterus Species*

	Sbr. [†]	<i>Dinotopterus</i> (1) and (2) (cm.) "G.A." [‡] (c.c.) Fil. [‡]	H.L. (cm.) "G.A."	<i>Dinotopterus</i> (3) (c.c.) Fil.	H.L. (cm.) "G.A."	<i>Dinotopterus</i> (3) (c.c.) Fil.
<i>C. mossambicus</i> .	11·5 191 18·0 601	12 80 —	<i>D. illesi</i> • •	18·2 1,556 20·0 1,858	25 — 54 —	<i>D. filibravis</i> • 21·0 <i>D. euryodon</i> • 13·7
	18·8 638 23·5 961	58 110 — 115	<i>D. loweae</i> •	29·5 1,714 14·7 813 19·8 1,660	56 — 14 14 80 —	29·0 4,443 <i>D. cumingtoni</i> • 13·3 26·0 5,641
<i>C. lazera</i> •	15·7 414 24·8 708	21 100 151 100	<i>D. longibarbis</i> • 16·5 1,230 <i>D. gigas</i> • 19·5 1,533	23·2 3,081 21·7 2,830	84 — 43 —	11·7 1 6·3 119 —
	11·0 217	11 —		26·3 3,560 28·0 5,324	60 — — —	6·5 117 1 5·7 1,698 —
<i>C. mellandi</i> •					<i>D. jacksoni</i> • 20·5 2,319 <i>D. foveolatus</i> • 12·6 645	24 180 21 3,347
				19·7 2,022 19·7 3,174	15·0 23·0 1,228	21 3,347 43 2,745 —
<i>D. atribranchus</i> • 11·1	603	2	—			12·3 148

The species of *Dinotopterus* are grouped in two major classes corresponding to the type of arborescent organ developed. The first class corresponds to groups 1 and 2 of Table I, the second to group 3.

* "Gill-area"; see text, p. 238.

† Volume of suprabranchial cavity (arborescent organs removed if developed).

‡ Number of filaments on the first gill-arch.

§ All species with hypertrophied arborescent organs.

terus bear the same relationship to those of *C. (Heterobranchoides)* species as do the reduced arborescent organs found in the subgroup *Clarias* (*Allabenchelys*), (see David, op. cit.).

Interspecific variation in the volume of the suprabranchial cavity is moderately high, but only four species have an obviously shallow chamber (see Table II). In all *Dinotopterus* species the "gill-fans" are fully developed.

Interspecific variability is not confined to gross structures but also occurs in the histology of the epithelium lining the cavity. Indeed, apparently novel arrangements of certain tissues are found in some *Dinotopterus* species, although it should be remembered that this aspect of the suprabranchial organ has not been studied at all intensively.

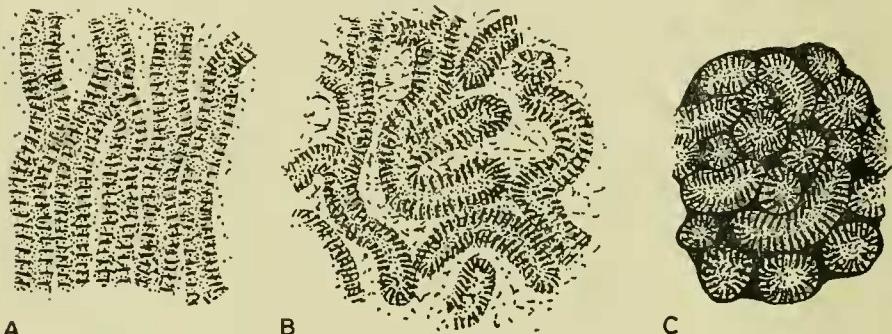


FIG. 1. Fragments of suprabranchial lining epithelium seen in surface view, showing the three types of lamellar organization. A. "Clarias"-type; B. "Saccobranchus"-type; C. "coralline"-type. Magnification c. 50 X.

Reference should be made to Rauther (1910) for a full and well-illustrated account of the histology of the suprabranchials in the Clariidae. As this author demonstrated, the epithelium lining the suprabranchial cavity of *Clarias* and the air chamber of *Saccobranchus* (= *Heteropneustes*) is differentiated into branchial and non-branchial tissue. The branchial tissue, which is arranged along the numerous blood-vessels, has the histological structure of normal gill-lamellae, save for the absence of gill rays. In the *Clarias* which I have examined (*C. mellandi*, *C. mossambicus*, *C. carsoni*, *C. pachynema*, *C. salae*, *C. jaensis*, *C. hilgendorfi* and *C. dumerili*) the suprabranchial lamellae are arranged in a basically linear but gently sinuous fashion (see Text-fig. 1A). This distribution of suprabranchial lamellae I have named the "Clarias" type or pattern. A second pattern is that found in the air-sac of *Heteropneustes* (see Rauther, op. cit., fig. 22). Here, the linear arrangement is obscured by the extreme sinuosity of the lamellae. A very similar pattern occurs in the suprabranchial epithelium of several *Dinotopterus* species (see Text-fig. 1B, and Table I); it differs slightly from the *Heteropneustes* type inasmuch as the lamellae are shorter and more irregularly arranged. This type of tissue occurring in *Dinotopterus* I have called the "Saccobranchus" type.

Yet a third pattern is found in *Dinopterus*. In this type (the "coralline"), many lamellae have, as it were, contracted and formed small, circular or ovoid patches of gill tissue interspersed amongst the less numerous patches of elongate lamellae. In contrast to the "Saccobranchus" type, there is much less inter-lamellar tissue in the "coralline" type of epithelium (see Text-fig. 1C). A further peculiarity in two of the five species with "coralline" epithelium is the heavy concentration of melanin deposited in the inter-lamellar tissue. As a result, the suprabranchial chamber is black except for the patches of gill tissue. Some melanin is found between the lamellae in other species but in none does it reach sufficient density to colour the epithelium.

Taking the "Clarias" pattern as basic, a comparison of the three types of suprabranchial epithelium suggests that the others could have evolved by a process of folding and fragmentation of the originally linear lamellae. Evidence from *D. cunningtoni* (see p. 220) seems to support this idea, at least for ontogeny.

Correlating the type of suprabranchial epithelium with the type of arborescent organ present, shows that (i) The "Clarias" type only occurs in species in which both trees are present and well- or moderately well-developed. (ii) Species without trees or with mere stumps on the fourth arch have either the "Saccobranchus" or "coralline" types of epithelium. (iii) The "Saccobranchus" pattern also occurs in species with well- or poorly-developed trees (see Table I). No adaptive value for any particular type of epithelium is immediately suggested by this analysis. That question is unlikely to be answered until we know more about the physiological significance of the suprabranchial organ in these essentially deep-water species.

When compared with the definitive condition in *Clarias*, the suprabranchial region in *Dinopterus* shows a wide range of developmental types. The question then arises: are these stages representative of a regressive or a developmental phase? This question is not readily answered but must be considered.

Evidence from comparative anatomy and ontogeny is somewhat equivocal but, I believe, suggestive of regression from the *Clarias* and *Heterobranchus* condition. *Dinopterus* is most closely related to *Clarias* and, more distantly, to *Heterobranchus*. In both these genera the suprabranchial organ is complete and well-developed, at least in adult and near-adult fishes. Species of both genera are virtually restricted to shallow waters of lakes, rivers and certain types of swamp. By inference from experiments made on several *Clarias* species (see below), the species are dependent on the suprabranchial structures as aerial respiratory organs; purely aquatic respiration is insufficient to fulfill their respiratory requirements. Species of *Dinopterus* on the other hand, are characteristic of deep-water habitats although some have a wide vertical range, which includes the pelagic as well as benthic zones (Jackson, 1959). For fishes living at depths of 40–70 metres, dependence on aerial respiration would be a severe handicap. Indeed it would probably prevent the invasion of these depths. Since the original fish-fauna of Africa would be essentially one of rivers and swamps, it seems that the trend in *Dinopterus* is one leading away from an adaptation to such habitats and towards a bathypelagic and benthic existence. Deep-water habitats can be looked upon as relatively "youthful" because the East and Central African lakes are geologically young features, certainly

post-dating the primary distribution of freshwater fishes over the continent.

A second indirect approach to this problem is afforded by the vertical distribution of the Nyasa species. No general correlation exists between the type of suprabranchial organ and the depths at which the species occur. Thus, and rather unexpectedly when compared with *Clarias*, at least one pelagic and one partly pelagic *Dinotopterus* species is without arborescent organs; in contrast, one deep-water species (*D. gigas*) has well-developed trees. Furthermore, developed trees are found in three species whose range extends from the pelagic zone down to a depth of 50 metres. These data strongly suggest that the species involved have broken away from the obligatory aerial respiration which restricts the vertical distribution of *Clarias* and *Heterobranchus* to shallow water. Once this physiological step has been taken, the stage is set for the regression of organs primarily concerned with air-breathing. It is interesting to note that three species found at the greatest depths, and which have not been recorded from the pelagic region (*D. foreolatus*, *D. filicipinnis* and *D. rotundifrons*), are all without arborescent organs and the volume of the suprabranchial cavity is greatly reduced.

The means whereby this breakaway from obligatory air-breathing was achieved, is discussed below.

PROBABLE METHODS OF RESPIRATORY COMPENSATION IN *DINOTOPTERUS*

Many experiments on several *Clarias* species (Boake, 1865; Das, 1927; and personal observations) all indicate that the suprabranchial organs are essential for life in this genus, the nearest living relative of *Dinotopterus*. Even in well-aerated water *Clarias* are apparently incapable of sustaining themselves by purely aquatic respiration. Hora (1935) is the only worker to claim that *Clarias* is not asphyxiated if it is kept in well-aerated water. Unfortunately, none of the authors investigating this phenomenon has cited the actual oxygen tensions of the water in which the fishes were kept. Personal field observations on *Clarias mossambicus* in Lake Victoria strongly suggest that even in the well-oxygenated waters of the Lake (O_2 concentrations 6–7 p.p.m.; 85–100% saturation) larger individuals (c. 50–80 cm. long) are forced to utilize their aerial respiratory organs. From this, I can only conclude that if purely aquatic respiration is possible, then the water would have to be oxygenated to an extent not generally encountered in the usual habitats of the species.

No *Dinotopterus* species has such well-developed suprabranchial arborescent organs as are found in *C. mossambicus* nor is there any indication that the oxygen concentrations occurring in Lake Nyasa are much greater than 7 p.p.m. (Beauchamp, 1953). Furthermore the depths at which most species occur is such that it seems impossible for the species to utilize the organs for surface air-breathing.

Some compensatory device is clearly involved and, as would be expected, this involves an increase in the surface area of the gills. The gills in all *Dinotopterus* species are considerably larger than those of equivalent sized *Clarias* (see Table II). The increase in area has been achieved both by elongation of the filaments and an increase in the number of filaments per arch. In large specimens there are about

50–70% more filaments on the first arch than in a comparably sized *Clarias*. As far as I could determine, the number of lamellae per millimetre of filament is approximately the same in large fishes of both genera.

The data given in Table II are admittedly crude but nevertheless clearly show intergeneric differences in gill size as well as interspecific differences within *Dinotopterus*. As a basis for size comparison I have chosen head length, principally because most of the larger *Clarias* material is of heads only. The character "gill area" was measured by tracing the outline of the filamentous part of the first gill arch (excluding the "gill-fans") onto squared paper divided into millimetre units. The results, therefore, by no means reflect the true surface area of the gill, but are merely a convenient way of indicating the size differences in this gill. It is obvious that with these crude measurements the figures obtained cannot be compared with the exact measurements given by Gray (1945) or Saxena (1958) for the gill areas of various marine and freshwater fishes.

The volume of the suprabranchial cavity was measured by filling the chamber with fine lead-shot; in those species (particularly *Clarias*) with expansive arborescent organs, the organs were removed before determining the volume.

Data in Table II show not only the remarkably larger gills of *Dinotopterus* but also several points in connection with the volume of the suprabranchial cavity, its correlation with gill area and its relationship to head size in the different species.

With so few specimens it is difficult to generalize on intraspecific variation in the volume of the cavity, which may be greater than appears from these figures. In the *Clarias* species studied, the suprabranchial cavity is large and becomes relatively larger with the growth of the individual. This allometric relationship is also shown by all species of *Dinotopterus*. In two species (*D. illesi* and *D. loweae*) the volume of the cavity is equivalent to that of *Clarias mossambicus* and *C. lazera*, at least in fishes with a head length of 14–20 cm.; but in larger *D. loweae* (H.L. 23–26 cm.) the cavity is relatively smaller. Only one species, *D. longibarbis* (represented by a single specimen), has a suprabranchial cavity relatively larger than that of *Clarias*. All other *Dinotopterus* species have the cavity smaller than in *Clarias* and in some (*D. foveolatus*, *D. rotundifrons* and *D. cunningtoni*) very considerably smaller both in relation to *Clarias* and to other *Dinotopterus* species.

With one exception, in all the *Dinotopterus* species compared there is a weak inverse correlation between "gill area" and cavity volume; even species within the group having the most reduced cavities show this relationship.

The functional significance of the suprabranchial cavity in *Dinotopterus* has not been investigated. That the cavity is highly vascular and predominantly branchial in its histology, strongly suggests that it serves some respiratory function. Jackson (1959) reports sighting several species feeding at the surface. In these species and under such circumstances, the suprabranchial organ may still function as a means of aerial respiration. But the vertical range of the same species also extends to the deep water and there are those species which apparently never leave the depths. Under such circumstances, the suprabranchial epithelium may serve as an aquatic respiratory surface. Hora (op. cit.) has shown that, if emptied of air, the aerial respiratory organs of *Ophiocephalus*, *Anabas* and *Amphipnous* can serve as gills.

It is, of course, essential that the cavities be largely emptied of air and I can see no reason to believe that this could not happen in *Dinotopterus*, especially when the fish is subjected to pressure. The valve system formed by the "gill-fans" is not particularly muscular and water under pressure should easily flood the suprabranchial chamber. The shape of the cavity and the arrangement of the valves are such that little or no air could remain trapped in it.

The four species with the proportionately smallest suprabranchial cavities (*D. filicarbis*, *D. rotundifrons*, *D. foveolatus* and *D. cunningtoni*) all have suprabranchial epithelium of the "coralline" type. The significance of the relationship has still to be determined. The only other species with "coralline" epithelium is *D. euryodon* but here the cavity is relatively large. Altogether there is little correlation between tissue-type and cavity size, except the negative one that "Clarias"-type epithelium is not found in species with a reduced chamber and tends to be associated with large arborescent organs. "Saccobranchus"-type tissue, on the other hand, occurs in both large and small chambered species but is commonest in the group of species which have reduced arborescent organs or are without these structures.

SUPRABRANCHIAL REGRESSION IN OTHER CLARIIDAE AND A COMPARISON WITH *DINOTOPTERUS*

The regressive series represented in descending order of suprabranchial organization by the genera and subgenera *Heterobranchus*, *Clarias* (*Heterobranchoides*), *C.* (*Clarias*), *C.* (*Allabenchelys*), *Chanallabes*, *Clariallabes*, *Gymnallabes* and *Tanganikallabes* (the organ is absent in *G. thioni* and *T. mortiauxi*) is well known and need not be elaborated upon here (David, op. cit.; Marlier, op. cit.; Poll, 1942b; Greenwood, 1956). Three points, however, should be noted; first, the series shows an overall decrease in maximum size; second, the body becomes increasingly anguilliform and third, the trend also involves the regression of certain roofing bones in the skull. Indeed, this series has been interpreted as an example of evolution through neoteny (Poll, 1942b; Greenwood, 1956).

Another unrelated example of suprabranchial regression is provided by the genus *Xenoclarias*, at present known from two deep-water species in Lake Victoria (Greenwood, 1958). In this genus, there is no suprabranchial cavity, no arborescent organs and the "gill-fans" do not develop. Instead, the upper filaments of each gill arch retain their filamentous nature. Unlike the more regressed members of the *Clarias* → *Tanganikallabes* line, *Xenoclarias* does not show any neotenic characters. Apart from its peculiar branchial arrangements it is a typical member of the subgenus *Clarias* (*Clarias*), although its adult size is small (15–16 cm. S.L.).

As David (op. cit.) first pointed out, the small size of fishes with regressed suprabranchials would enhance the possibility of cutaneous respiration and thus provide some compensation for the loss of the aerial respiratory organs. In *Xenoclarias*, besides increased surface area relative to volume there is an increase in gill surface because the "gill-fans" are suppressed.

The species of *Dinotopterus* provide yet another line of suprabranchial regression which differs in certain respects from the other two. An outstanding difference is

the large adult size of all *Dinotopterus* species, amongst which are to be found some of the largest Clariidae. Clearly, increased cutaneous respiration is not a compensating respiratory mechanism in these fishes ; increased gill area, however, seems to be the factor involved (see p. 237 and Table II).

The state of the suprabranchial organ in a few of the less regressive *Dinotopterus* (group I in Table I) is comparable with that of certain *Clarias* (*Allabenchelys*) *dumerili*; other species of this subgenus, the most regressive of the *Clarias*, have arborescent organs relatively larger and more complex than *Dinotopterus*. I have found regressed arborescent organs in only one population of *Cl. (A.) dumerili*, that occurring in the Cuvo River, Mount Maco, Angola. Other populations of this species have arborescent organs typical of the subgenus, of which the following species were dissected : *C. carsoni*, *C. submarginatus*, *C. philipsi*, *C. longior*, *C. poensis*, *Allabenchelys longicauda* and *All. brevior*). Likewise, the relative development of the suprabranchial organ in *Chanallabes* species is greater than in *Dinotopterus*. In certain respects, namely the absence of arborescent organs and a decrease in the volume of the cavity, the suprabranchials of *Clariallabes petricola* and *Dolichallabes microphthalmus* compare with the majority of *Dinotopterus* species ; in *Cl. petricola*, however, the "gill-fans" are less developed. The only clariid species which seem to show regression in the suprabranchials even greater than that of *Dinotopterus* are *Gymnallabes thioni* and *Tanganikallabes mortiauxi* (see Poll, 1942a ; 1953).

CONCLUSION

Regression of the suprabranchial respiratory organs has been achieved in many species of Clariidae. The manner of their decline and the provision of compensatory means of respiration show considerable variation, but all seem to involve heterochronic growth either affecting the organs alone or the entire skull. Species with reduced suprabranchials are found in a great variety of habitats including swamps, fast flowing rivers and the deep waters of lakes. Those species with elongate bodies have even invaded such habitats as the interstices of rocks and coarse gravel on river beds. As a group the "regressive" clariids have probably proved more successful (as measured by variety of habitat) than those species and genera which have retained a fully-developed suprabranchial organ and the concomitant obligatory air-breathing habit. Geographically, however, their distribution is limited to the approximate area of 5° N. to 15° S. as compared with the almost pan-African and Asiatic distribution of the fully air-breathing species (see David, op. cit.).

This study has not thrown much more light on the evolution of air-breathing organs in the Clariidae. However, from what has been said it is clear that I support Beadle's (1932) views on the environmental conditions favouring the origin and development of such structures. Beadle supposed that aerial respiration was of considerable adaptive value to fishes living in near-stagnant and poorly oxygenated closed swamps. That is, swamps not connected with open water as are most present-day African swamps. He further supposed that closed swamps probably preceded the formation of the open type. The geological history of most African lakes certainly supports this interpretation of geomorphological events. Thus, invasion of open-

water habitats would perform take place at a later date and after the fishes had evolved an accessory aerial respiratory mechanism.

When reviewing Beadle's ideas, David (op. cit.) doubted this sequence of events, particularly since there is the implication in Beadle's paper that in open lake conditions, the suprabranchial respiratory organs would be redundant. As David comments, the highly developed accessory respiratory organs of *Heterobranchus* and *Clarias* hardly have the appearance of "Reliktorgane". But, from what we know of the respiratory requirements of *Clarias* this is literally what these structures are, organs developed in a different environment but now forming an integral part of the animal's physiology no matter what environment it may occupy. This interpretation of the suprabranchial organs in *Clarias* and *Heterobranchus* seems to answer David's objection and to link the ideas of both this author and Beadle. A truly regressive accessory respiratory organ is only seen, so I believe, in those Clariidae which have developed some compensatory respiratory mechanism (such as increased cutaneous respiration through decreased body-size, or enlargement of the gill area). With regard to these organs, the Clariidae as a whole may be an example of cyclic evolution. That is to say there has been the primary evolution of an aerial respiratory organ to meet the challenge of a severely deoxygenated environment and then, in certain branches, the loss of these structures when a new set of moderately well-oxygenated habitats were themselves evolved and were available for exploitation.

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